Sensory and cognitive adaptations to social living in insect societies

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A key question in evolutionary biology is to explain the causes and consequences of the so-called "major transitions in evolution," which resulted in the progressive evolution of cells, organisms, and animal societies (1–3). Several studies, for example, have now aimed to determine which suite of adaptive changes occurred following the evolution of sociality in insects (4). In this context, a long-standing hypothesis is that the evolution of the spectacular sociality seen in insects, such as ants, bees, or wasps, should have gone hand in hand with the evolution of more complex chemical communication systems, to allow them to coordinate their complex social behavior (5). Indeed, whereas solitary insects are known to use pheromone signals mainly in the context of mate attraction and species-recognition, social insects use chemical signals in a wide variety of contexts: to communicate their caste or reproductive status, recognize nestmates from invaders, mark the way to food sources, or alarm nestmates about imminent danger (5). Well-controlled studies of the change in investment in chemical communication systems in highly eusocial insects, such as ants, termites, or Corbiculate bees, however, have proven hard to conduct, because eusociality in these taxa evolved long ago in the Cretaceous (6) and closely related solitary species are no longer around (Fig. 1). In PNAS, Wittwer et al. (7) now provide an elegant solution to this problem. By studying Halictinae sweat bees—a group of primitively eusocial insects that evolved sociality more recently and on several occasions reverted back to a solitary lifestyle (8) (Fig. 1)—they succeed in making an accurate comparison of the investment in chemosensory systems made by social and derived, closely related, nonsocial species.

Halictinae sweat bees are unique in that they display a diverse array of behavioral repertoires that range from solitary nesting to communal group living—where females share the same burrow but where all eventually reproduce—and fully eusocial lifestyles, sometimes accompanied by a certain amount of queen–worker caste size-dimorphism (9). Other species, like *Lasioglossum albipes*, are still socially polymorphic, and can either nest solitarily or form small annual colonies, depending upon their environment (9). And one species, *Lasioglossum marginatum*, is even known to form large perennial eusocial colonies of over 400 workers (9). By comparing data from over 30 Halictine bees with contrasting levels of sociality, Wittwer et al. (7) now show that, as expected, social sweat bee species invest more in sensorial machinery linked to chemical communication, as measured by the density of their antennal sensillae, compared with species that secondarily reverted back to a solitary lifestyle. In fact, the same pattern even held for the socially polymorphic species *L. albipes* if different populations with contrasting levels of sociality were compared (Fig. 1, *Inset*). This finding suggests that the increased reliance on chemical communication that comes with a social lifestyle indeed selects for fast, matching adaptations in their sensory systems.

Interestingly, Wittwer et al. (7) further show that in the social polymorphic sweat bee *L. albipes*, odor profiles show consistent differences between social and solitary populations. A prediction not explicitly tested by the authors though is if social species also invested in the production of chemically more complex signals. Surprisingly, a recent study of over 200 species of Hymenoptera (10) found no evidence of sociality being linked with the emission of more complex chemical signals. Nevertheless, this study used less-advanced comparative methods than Wittwer et al. (7), and the result appeared to be mainly driven by the chemically very diverse profile displayed by parasitic Hymenoptera, where diverse chemical signals appear to be required for mate recognition, and where chemoreception is very important because of its role in finding potential mates and hosts and avoiding harmful substances in the environment (11). In the future, a more extensive study of chemical signal complexity in clades containing both social and closely related solitary species, such as Halictinae sweat bees or Xylocopinae carpenter bees (Fig. 1), would alleviate this problem. This would then allow us to test if increased investment in chemosensory machinery is or is not linked with the emission of more complex chemical messages. Other independent evidence, at least, suggests that it is. The evolution of complex chemical signaling in social

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The authors declare no conflict of interest.
See companion article 10.1073/pnas.1620780114.
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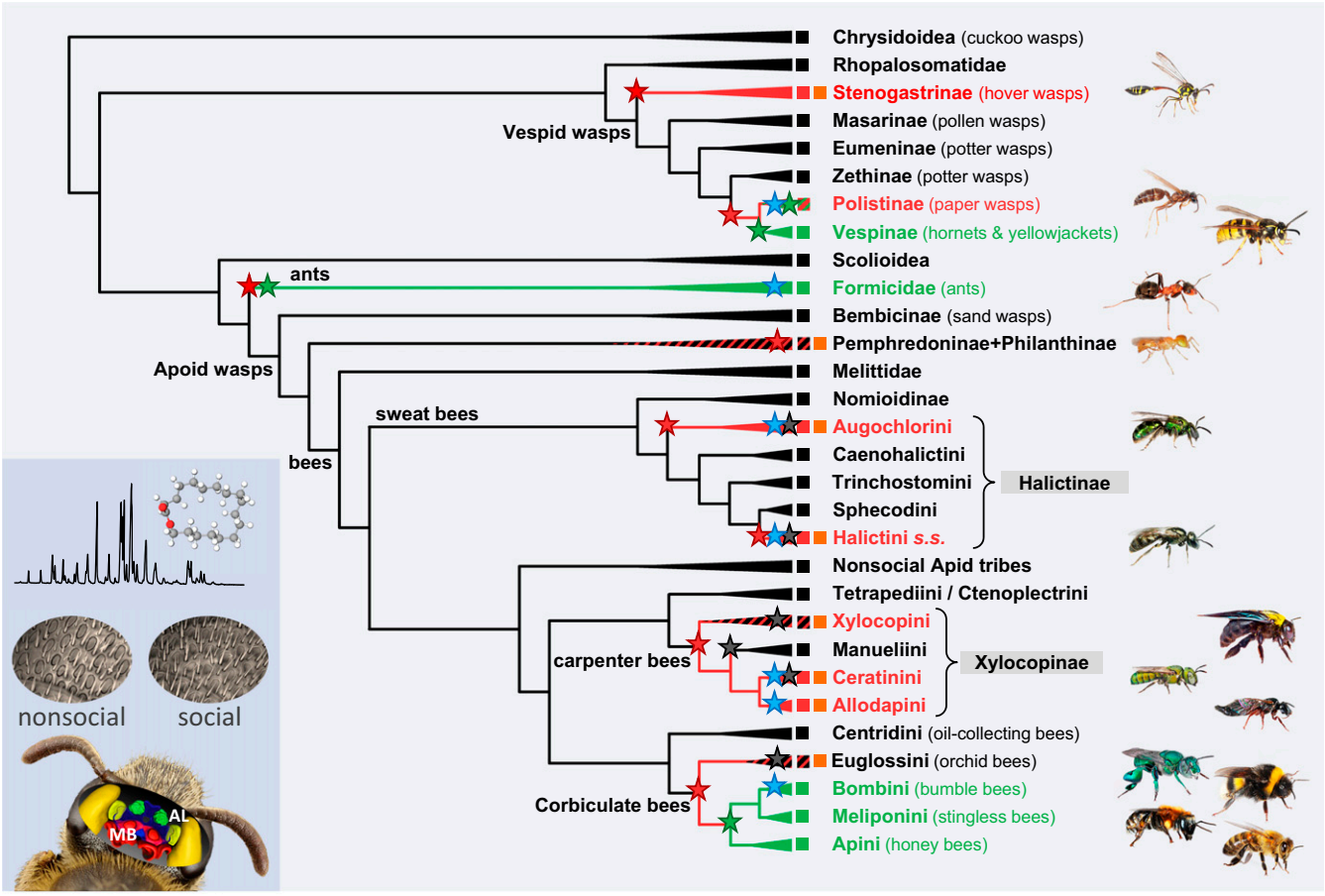

Fig. 1. Cladogram showing the independent origins and secondary losses of sociality in the Hymenoptera (after refs. 6 and 20–24). For clarity, only a selection of the closest solitary outgroups are shown. Red, blue, and green stars represent origins of species with behaviorally defined castes, species with weak caste dimorphism but totipotent workers (still capable of mating), and species with an obligate worker caste (unable to mate). Note that some swarm-founding Polistinae evolved an obligate worker caste and that in some ants and a few bumblebee species, workers secondarily regained the ability to mate. Social species shown: *Eustenogaster* sp., *Agelaia vicina* (queen), *Vespula vulgaris* (queen), *Formica polyctena* (worker), *Microstigmus comes*, *Augochlorella pomoniella*, *Lasioglossum zephyrum*, *Xylocopa aestuans*, *Ceratina smaragdula*, *Exoneurella tridentata* (queen), *Euglossa dilemma*, Bombus *lucorum* (worker), *Melipona subnitida* (worker), *Apis mellifera* (worker), and *Lasioglossum albipes* (*Inset*). In PNAS, Wittwer et al. (7) used data from Halictini sweat bees to show that sociality is strongly associated with investment in sensorial systems linked to chemical communication, and that species that secondarily reverted back to a solitary lifestyle reduce investment in costly sensorial machinery. This is shown (*Inset*), for example, in the reduced density of antennal sensillae observed in females of the nonsocial vs. the social form of *Lasioglossum albipes* (*Middle*). Sensillae detect incoming chemical signals (*Top*), after which they are integrated in the antennal lobes (AL) and processed in the brain's mushroom bodies (MB) (*Bottom*). Photographs courtesy of Zestin Soh (*Eustenogaster* sp., *C. smaragdula*, *X. aestuans*); Robert Matthews (*M. comes*); Gary McDonald (*A. pomoniella*); Alex Surcică (*L. zephyrum*); Caroline Harding and Museum Victoria (*E. tridentata*); Sam Droege (*L. albipes*); and T.W. (remaining species); and scanning electron micrographs courtesy of Sarah Kocher.

insects, for example, has been shown to be associated with a diversification of the exocrine gland repertoire (12). Ants, for example, evolved the metapleural gland and the postpharyngeal gland anew, and the social Corbiculate bees evolved wax glands, used both for nest construction and chemical communication (12). Likewise, a population genomic study of the honey bee genome showed strong signs of positive selection on genes coding for enzymes involved in cuticular hydrocarbon biosynthesis (13), and genomic studies that compared social and nonsocial insect species have found that genes involved in exocrine gland development evolve unusually fast in social insects (14). Furthermore, gene families involved in chemical communication in ants have been shown to be greatly expanded (15), and families of odorant receptors expanded in some, though not all, lineages of highly eusocial bees (16) and have been shown to be under unusually strong selection in social lineages (11).

Apart from increased investment in communication, it has also been suggested that sociality could select for an increased brain capacity, because social behavior typically imposes additional cognitive challenges, a theory known as the "social brain hypothesis" (17, 18). This theory appears to fit well for several orders of mammals and birds, where social behavior often requires individual recognition and brain capacity positively correlates with group size (17). Surprisingly though, in insects, this hypothesis does not seem to hold as well. In fact, the exact opposite pattern has been documented in vespid wasps, where the relative size of the mushroom bodies—the part of the brain that is involved in processing signals and long-term memory—is smaller in social Polistinae paper wasps than in their solitary Eumenine potter wasp cousins (17). One explanation may be that social insects gain their intelligence mainly through sheer number, via simple processes of

self-organization, which require only limited cognitive ability. On the other hand, in an intraspecific comparison of the social and solitary form of the Halictine bee *Megalopta genalis*, the social reproductive females were found to have larger mushroom bodies than workers or solitary reproductives (19). Perhaps, then, bees did evolve more complex brains as they became more social, and it is only wasps that rely on collective "swarm intelligence."

Recently, solid large-scale phylogenies have become available of all of the major social insect groups and their direct solitary ancestors (6, 20–24) (Fig. 1). With these evolutionary trees in hand, it will be exciting to see how many more comparative analyses—like the one of Wittwer et al. (7)—will become feasible, and how this will shed light both on the fundamental factors that have driven the evolution of sociality (3), as well as on the major changes that insects underwent in their transition toward more complex sociality (4).

Acknowledgments

We thank Fabio Santos do Nascimento for providing an *Agelaia vicina* specimen to photograph. This study was supported by Fund for Scientific Research-Flanders Grant G.0A51.15 and KU Leuven Centre of Excellence Grant PF/2010/007 (to T.W.), and Fund for Scientific Research-Flanders Postdoctorate Grant 12Q7615N (to J.S.v.Z.).

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